



Listening to orthoptera in agroforestry: methodological and management insights for conservation

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Abstract Biodiversity, particularly insects, faces considerable threats in intensively managed agricultural landscapes. Agroforestry systems (AFS), which integrate woody elements into agricultural land, can enhance biodiversity. This study aims to identify management factors influencing orthopteran richness and abundance in AFS. Additionally, it evaluates the utility of passive acoustic monitoring (PAM) for orthopteran detection by comparing it to field monitoring. Orthopteran monitoring was conducted at 20 silvoarable AFS in western Switzerland. Orthopteran richness was recorded using transects and PAM, while abundance was obtained only from transects. Both methods yielded similar species numbers. Daytime PAM detected cryptic or low-abundance species missed by daytime transects but failed to record one non-stridulating and some nocturnal species. Consequently, data from both methods were combined to provide a more comprehensive analysis of factors influencing orthopteran richness. The analysis revealed that increasing plant species diversity within the understory vegetation strips (UVS) had a positive, though not statistically significant, effect on orthopteran species richness. Furthermore, a non-significant reduction trend in orthopteran abundance was observed in conventionally managed agroforestry systems compared to organically managed ones.

Implications for insect conservation Our study shows that PAM can effectively monitor orthopteran richness in AFS. By increasing plant diversity in UVS and through organic management, farmers can enhance orthopteran richness and abundance in AFS and support biodiversity conservation.

Keywords Orthoptera · Agroforestry · Passive acoustic monitoring · Insect · Biodiversity · Switzerland

Introduction

The growing demand for food, driven by an increasing global population, has intensified agricultural practices that rely heavily on pesticides and fertilizers, contributing to global warming and groundwater pollution (Schmidt et al. 2021). Furthermore, modern intensified agricultural practices are a major driver of biodiversity loss. This results from the increased use of fertilizers and pesticides, as well as the removal of semi-natural landscape elements to facilitate management, which reduces landscape complexity (Meier et al. 2022). The decline in biodiversity and habitat quality affects many animal groups, including orthopterans. Currently, 31.3% of all Orthoptera species in Germany are classified as threatened (Poniatowski et al. 2024), while in Switzerland, 39.2% of the 105 native species (i.e. 40 species) were considered under threat in 2007 (Monnerat et al. 2007).

Agroforestry, an agricultural practice, integrates perennials (trees and shrubs) with agricultural crops (woody or

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non-woody) and/or livestock within the same land management unit, often arranged in specific spatial patterns (Rigueiro-Rodríguez et al. 2009). The integration of trees into agricultural land enhances environmental benefits, such as reducing nutrient loss, increasing carbon sequestration, and minimizing soil erosion (Alam et al. 2014). Moreover, agroforestry has the potential to promote biodiversity by providing structures and habitats for a variety of species (Kletty et al. 2023). In Switzerland, traditional agroforestry systems like “Wytweiden” in the canton of Jura and “Selven” in the canton of Ticino—where single trees are integrated into pastures in a scattered spatial arrangement (Kay et al. 2019)—positively affect biodiversity (Baur and Stingelin 1997). However, due to economic and management constraints, these traditional systems are in sharp decline (Eichhorn et al. 2006). Consequently, modern agroforestry systems have been developed to align with current agricultural practices, incorporating trees planted in rows (alley cropping) to facilitate machinery movement and optimising crop shading (Rigueiro-Rodríguez et al. 2009). Today, most modern agroforestry practices in Switzerland are silvopastoral and silvoarable practices (Kay et al. 2020). Silvopastoral practices combine trees with livestock, while silvoarable practices contain widely spaced trees inter-cropped with annual or perennial crops (Mosquera-Losada et al. 2009). Like the traditional agroforestry systems, the modern silvoarable systems have a positive impact on biodiversity conservation by increasing the abundance or diversity of small mammals (Klaa et al. 2005), birds (Gibbs et al. 2016), carabids (Boinot et al. 2019b), and pollinating insects (Varah et al. 2013; Kletty et al. 2023). The understory vegetation strips (UVS) within silvoarable agroforestry systems provide habitat or refuge for many plant and animal species and explain the positive effect on the diversity of many taxonomic groups (Boinot et al. 2019a, b; Kletty et al. 2023).

In grassland, orthopterans contribute to more than half of the total arthropod biomass in the grass layer (Gardiner et al. 2005b). At local scale they are an essential part of the diets of many spiders (e.g. families Araneidae, Agelenidae, Linyphiidae) and birds (e.g. *Ciconia ciconia*, *Lanius collurio*, *Falco tinnunculus*) (Ingrisch and Köhler 1998; Gardiner 2018). Given their important role in grassland systems, orthopterans are likely crucial for the positive impact on biodiversity in silvoarable agroforestry systems. Identifying the factors influencing the habitat quality of UVS to support the abundance and the diversity of orthopterans is therefore important. Factors influencing habitat preferences for orthopterans in grassland—and likely, the presence of certain orthopteran species within UVS—include oviposition site selection, food preferences, vegetation structure, and management practices (Gardiner 2018). These influencing factors are complex and inter-related (Gardiner 2009).

However, despite the significant ecological importance of orthopterans (Poniatowski et al. 2024), the potential of modern agroforestry systems to promote orthopteran abundance and diversity has received little research attention (Kletty et al. 2023). Moreover, it remains unclear whether the factors mentioned above specifically impact orthopteran populations within these systems (Kletty et al. 2023).

Several methods are available for sampling the species composition of grassland orthopteran diversity, including sweep netting, biocenometer, and line transect (Gardiner et al. 2005b). Each method has its advantages and disadvantages, but they all share the common traits of being time-intensive and invasive (Gardiner et al. 2005b). Passive Acoustic Monitoring (PAM) is a non-invasive method that uses autonomous recording units (ARUs) to capture acoustic recordings over a specified period (Wood et al. 2021). PAM is commonly used for monitoring birds and bats and offers a promising solution for studying stridulating insects such as orthopterans (Obrist et al. 2010). Stridulation evolved as an energetically efficient method of communication, allowing orthopterans to attract potential mates (Roesti and Keist 2009). The structure of the song is crucial for an efficient mate recognition system (Penone et al. 2013b) and can be visualized on an oscillogram through species-specific changes in loudness (Roesti and Keist 2009). Consequently, Orthoptera songs have a remarkable level of stereotypy and reliability, making them good taxonomic indicators (Baur et al. 2006; Roesti and Keist 2009). Additionally, the large number of stridulating species among orthopterans allows a broad species detection in an economical and non-invasive manner (Riede 2018). Therefore, some studies have used bioacoustic recorders to identify orthopteran species compositions within different ecosystems (Berggren et al. 2001; Chesmore and Ohya 2004; Penone et al. 2013a, b; Bennett et al. 2025). So far the recordings of stridulating orthopterans were analysed either by trained listeners (Penone et al. 2013a, b) or by automated programs (Chesmore and Ohya 2004; Newson et al. 2017; Faiss & Stowell, 2023, Bennett et al. 2025) identifying orthopterans at species level. Both methods are linked to challenges. While analyses by trained listeners are very time-intensive, automated programs could overcome this issue, but require enough baseline data for the respective species and region, which often do not exist (Riede 2018).

Thus, the aim of this study was (i) to test Passive Acoustic Monitoring (PAM) for determining orthopteran richness and (ii) to identify factors influencing their abundance and richness on 20 silvoarable agroforestry fields. Therefore, we used AudioMoth recording devices while also performing line transects in the field and compared the two methods. This approach facilitates the collection of data on

orthopteran richness while also providing insights into the effects of AFS design and management.

Methods and materials

Study area

This study was conducted as part of the ongoing project “Agro4esterie” (2020–2027), which aims to promote modern agroforestry systems in the western part of Switzerland. The project focuses on implementing these systems and analysing the effects on biodiversity (flora and fauna), weed pressure, soil health, and climate (Roberti et al. 2023). Twenty silvoarable agroforestry fields, all established in 2020, were selected for this study. The sites are located at elevations ranging from 318 m to 919 m over sea level in a temperate climate (Fig. 1). They vary in size (1–12 ha), number of UVS (1–11), total number of trees, tree species, and cultivated crops. Among these fields, twelve are managed organically, while eight are managed conventionally. Detailed information for each field can be found in Table S1.

Orthopteran monitoring

Line transect method

Two surveys were conducted at each of the 20 study sites, which were then pooled to ensure a comprehensive sampling of species across the season. The first survey was

conducted from July 22 to July 27, 2024, and the second from August 19 to August 23, 2024. During this period, most orthopteran species exhibit their peak imago abundance (Baur et al. 2006).

The line transects were used to visually sample orthopteran species richness and their abundance (Gardiner et al. 2005a; Gardiner and Hill 2006). The transect was always located within the UVS and was performed by the same person. To minimize edge effects, transects were never conducted in the outermost UVS and always began 10 m from the field edge. Depending on the agroforestry field design, transects were either performed in two different UVS (Design A, 10 sites) or sequentially within the same UVS, ensuring sufficient distance between them (Design B, 10 sites) (Fig. 2).

At each of the 20 agroforestry sites, the number of orthopteran species was determined in a two-step process. Firstly, during a 15-minute period, all orthopteran species found within the agroforestry site were recorded to generate a species list. This was conducted in the two outermost UVS, outside the transect line, to avoid disturbing subsequent transects (Fig. 2). The genera *Tetrix* and *Gryllus* were not noted due to their small size and their phenological peak of adults which is earlier in the season. The species identification was based on Coray and Thorens (2001), Baur et al. (2006), Bellmann et al. (2019) and Fischer et al. (2022). The nomenclature of the species followed the Orthoptera Species File Online database (Cigliano et al. 2024). Subsequently, two transects per site (each 2 × 50 m, 10 min) were walked to visually identify species and count orthopteran individuals (Fig. 2). Only visually confirmed records were included. Field surveys were conducted between 9 a.m. and

Fig. 1 Study sites in western Switzerland (20 silvoarable agroforestry fields). Yellow circles represent organically managed sites, and blue triangles represent conventionally managed sites



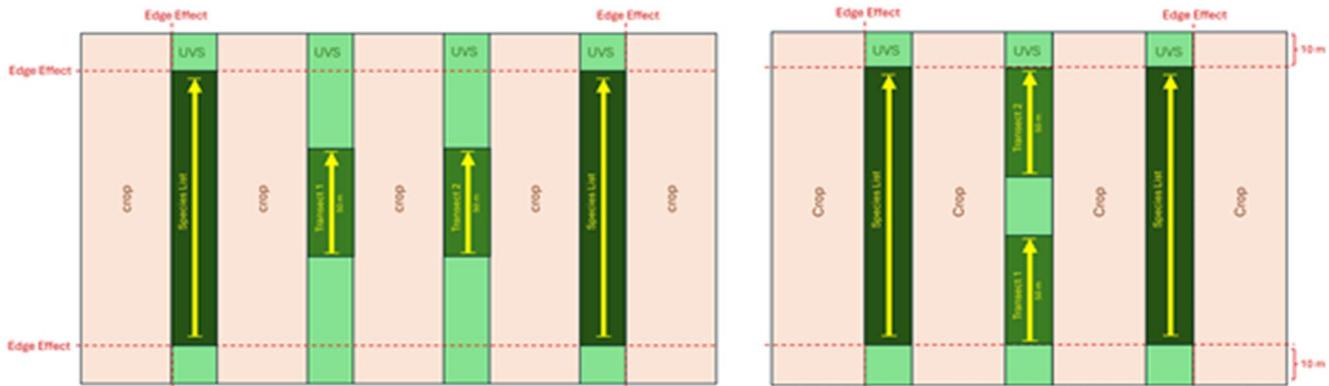


Fig. 2 Agroforestry field design. Species Lists were generated from 15 min of recording orthopteran species in the two outermost UVS. Transects recorded all orthopteran species and their abundances during a 10-minute walk along 2 × 50-m UVS band. Left: Design A, agrofor-

estry field design with more than three UVS; Right: Design B, agroforestry field design with three UVS. UVS: understory vegetation strip; crop: cropland

5 p.m. on days with temperatures above 15 °C, wind speed below Beaufort 4 (20–28 km/h), and a cloud cover of max. 50%. These parameters represent the activity maximum of grassland orthopterans, which reduces the number of undiscovered ones (König and Krauss 2019). The timing of transect walks and plot observations was systematically randomized to avoid day time bias (Klein et al. 2020). Distinguishing *C. biguttulus* from *C. brunneus* within a transect, especially females, is difficult (Baur et al. 2006). To ensure accurate identification within the transect, all individuals of both species were caught whenever possible. Escaped individuals were recorded as “*C. biguttulus/C. brunneus*” and later assigned based on the ratio of successfully captured and identified individuals at each site.

Passive acoustic monitoring (PAM)

To identify orthopteran species composition using PAM, recordings were made with AudioMoth recorders (Hill et al. 2019). In each of the 20 agroforestry fields, a recorder was placed within a UVS, centrally located in the field, at a height of approximately 1.5 m, where the transect was conducted. Each AudioMoth device recorded continuously for two hours twice daily (12:00–14:00 and 22:00–00:00 local time) from August 1 to August 10, 2024. These time frames were chosen to capture the majority of stridulating orthopterans (Roesti and Keist 2009). For the method comparison, only daytime recordings were used, whereas both daytime and nighttime recordings were used for the environmental factor analysis. Most stridulating orthopterans produce sounds within the frequency range of 2–40 kHz (Chesmore and Nellenbach 2001). Therefore, the recorders were set to a 192 kHz sample rate to ensure accurate capture, following the guideline to sample at least twice the highest frequency of interest. The song activity of some orthopteran species, such as *D. verrucivorus*, is significantly influenced by cloud

cover and temperature (Fischer et al. 1997). Therefore, temperature was recorded simultaneously by the AudioMoth device during audio capture and was used during the analysis of the recordings as a parameter for identifying orthopteran species.

To identify stridulating orthopterans within the recording protocol, 30-second audio snippets were extracted every 15 min. All snippets were downsampled by a factor of 4, from 192 kHz to 48 kHz, to reduce file size. With a sample rate of 48 kHz, frequencies up to 24 kHz (Nyquist frequency) are theoretically captured. The downsampling brings no disadvantage, as the human ear perceives frequencies only up to approximately 20 kHz (Dickreiter & Hoeg, 2023) and all expected orthopteran species within the study sites stridulate within this range (Roesti and Keist 2009), making them audible to the human ear. The recordings were analysed blind to the location to avoid bias, though the temperature for each snippet was known. The Species identification was conducted both acoustically and visually by a single observer. To assess accuracy, a subset of recordings was independently reviewed by a second observer. For visual analysis, the software Audacity v. 3.1.3 was used to examine the oscillograms. The identification of stridulating orthopteran species was based on Roesti and Keist (2009) using reference recordings of known species and their corresponding oscillograms (Roesti and Keist 2009).

Data analysis

Comparison of PAM and transect method

To compare the two monitoring methods, the number of orthopteran species detected per site was examined. Only daytime acoustic recordings were considered, as transect surveys were conducted exclusively during the day. All

analyses were performed in RStudio version 4.4.1. Detections from each method were visualized in a scatterplot using the ggplot2 package (Wickham 2016), with a 1:1 reference line. A Reduced Major Axis (RMA) regression (Harper 2016) was fitted using the lmodel2 package (Legendre and Oksanen 2024). Agreement between methods was evaluated by comparing the RMA slope and intercept with those of a 1:1 line (slope=1, intercept=0). Statistical agreement at $\alpha=0.05$ was established when the 95% confidence interval of the RMA slope included 1 and the 95% confidence interval of the RMA intercept included 0. Also, a paired Wilcoxon signed-rank test was applied to assess whether the number of species recorded differed significantly between the two methods. To explore species-specific detection patterns, a bar plot was generated using the ggplot2 package in R (Wickham 2016). This plot illustrates which orthopteran species were detected by each method, highlighting differences in detectability between transect surveys and daytime passive acoustic monitoring (PAM).

Environmental factors

To explain orthopteran richness and abundance, further data from the “Agro4esterie” project were utilized. Table 1 provides a brief explanation of all variables used. The following section describe how data for each variable were collected.

Data for the variables Plant Species Richness (PSR), Plant Species Heterogeneity (PSH), UVS Width (UW), and Soil Cover (SC) were collected during vegetation surveys conducted in 2023 within the UVS, following the methodology described by Roberti et al. (2023). The data for the

Table 1 All environmental factors used as explanatory variables in the models for OSR (orthopteran species richness) and OA (orthopteran abundance)

Explanatory Variable	Description
Plant Species Richness (PSR)	Total number of plant species within the UVS
Plant Species Heterogeneity (PSH)	Spatial distribution of plant species (Beta diversity) within the UVS
Soil Cover (SC)	Soil cover within the UVS [%]
Management (M)	Management type of agroforestry site [organic or conventional]
BPA 200	Biodiversity promotion area within 200 m radius [%]
BPA 500	Biodiversity promotion area within 500 m radius [%]
UVS Width (UW)	Width of the Understorey Vegetation Strip (UVS) [m]
Number of UVS (NOU)	Number of UVS per agroforestry site
Size (S)	Size of the agroforestry site [ha]
Disturbance (D)	Disturbance between orthopteran monitoring surveys (e.g., mowing) within UVS [yes/no]
Crop Type (CT)	Cultivated crop in 2024 [ley or not ley]

Biodiversity Promotion Areas (BPA) variables BPA 200 and BPA 500 were obtained using land use maps, which included Biodiversity Promotion Areas (BPA) and forest edge areas surrounding each agroforestry field (Geodienste 2023; Swisstopo 2024), using data of 2023. BPA included in the analysis are as follows: extensively used meadows, less intensively used meadows, litter meadows, extensively used pastures, wooded pastures, riparian meadows, species-rich areas in summering areas, conservation strips, beneficial insect strips, wildflower strips, rotational fallows, field margins, cereals in wide rows, vineyards with natural biodiversity, standard fruit trees, nut trees, site-appropriate individual trees, hedges, field and riparian woodland, ruderal areas, stone heaps and walls, dry stone walls, ditches, ponds, and region-specific biodiversity promotion areas (Agrinatur 2024). The first 10 m of the forest edge were counted as forest edge (Swisstopo 2024). The proportion (%) of the area within a radius of 200 (BPA 200) and 500 m (BPA 500) was calculated in QGIS (v.3.32).

Orthopteran species richness and abundance

To understand the factors influencing orthopteran species richness (OSR) and orthopteran abundance (OA), a multiple linear regression model was created for each dependent variable. For the dependent variable OSR, data from the line transect method and PAM were combined. Combining data from both methods provides a more comprehensive view of species composition at each site (Table S2) and offers better insight into the factors influencing orthopteran species richness in agroforestry systems. OA was determined by combining the number of individuals across all orthopteran species from both transects for each survey period, resulting in a count of individuals per 200 m² within the UVS. To account for seasonal changes in species abundance (Baur et al. 2006), these totals were then averaged across the two survey periods to use as the dependent variable in the model.

Table 1 presents the explanatory variables used in the models for both dependent variables. In addition, the following interaction terms were included as explanatory variables in both models: PSH × M (Management), PSH × SC, M × SC, PSR × M, PSR × SC and M × CT (Crop Type). An explanation of each interaction term is provided in Table S3. All other possible interactions were considered irrelevant for the purposes of this study and were therefore excluded from the models. The model analyses were conducted in RStudio 4.4.1 using multiple linear regression models with the *lm* function (Weaver et al. 2017).

To address potential overfitting of the two models, the *dredge* function from the multimodel inference (MuMIn) R package (Bartoń 2024) was used. Before this step a Spearman correlation matrix was generated among all explanatory

variables to check for collinearity. Variables with correlation coefficients above 0.7 were specified in the *dredge* function for exclusion, to ensure that only combinations of low-inter-correlation variables were tested (Dormann et al. 2013). The best model was selected based on the Akaike Information Criterion corrected for small sample sizes (AICc), with the lowest AICc score indicating the most appropriate model (Bozdogan 1987). The linearity for both models was assessed visually by plotting fitted values against residuals and analytically using the rainbow test with the *rainiest* function from the *lmtest* R package (Zeileis and Hothorn 2002). The residual distribution was checked visually with a Q-Q plot and tested analytically with the Shapiro-Wilk test. Explanatory variables with the lowest AICc scores were further examined visually using scatterplots or boxplots generated with the *ggplot2* package in R.

Results

Orthopteran species richness

Line transect method

A total of 13 orthopteran species were found with the line transect method. On average, 4.6 (± 1.5) species were identified per site. A maximum of six species per site were found at seven sites, while on one site only one species was found. The most common species were *C. biguttulus* (18 sites), *P. parallelus* (17 sites) and *R. roeselii* (13 sites). A complete list of recorded species using the line transect method is provided in Table S2.

Passive acoustic monitoring (PAM)

A total of 2586 snippets were extracted from the day and night audio recordings, amounting to 1290 min of audio. Only a few snippets could not be analysed due to heavy wind noise or unfavourable weather conditions, such as rainfall, during the recording period. In total, 16 orthopteran species were detected across 20 silvoarable agroforestry sites using both day and night recordings. Eleven species were recorded only during the day, while five were found exclusively at night (*T. viridissima*, *R. nitidula*, *P. falcata*, *O. pellucens*, *P. griseoptera*). On average, 6.3 species (± 1.7) were identified per site using both day and night recordings. In contrast, daytime recordings alone yielded an average of 4.0 species (± 1.3) per site. The most common species in day and night recordings were *T. viridissima* (20 sites), *P. parallelus* (19 sites), and *C. biguttulus* (18 sites). In daytime-only recordings, the most frequent species were *P. parallelus* (19 sites), *C. biguttulus* (18 sites), and *C. brunneus* (16 sites). A

complete list of species recorded using PAM is provided in Table S2.

Aggregated

Combining the number of species detected by both methods, a total of 19 orthopteran species were found on 20 silvoarable agroforestry sites. On average, 7.4 (± 2.0) species were identified per site. A maximum of eleven species per site were found at two sites, while on one site only three species were found. The most common species include *C. biguttulus* (20 sites), *T. viridissima* (20 sites) and *P. parallelus* (19 sites) (Table S2).

Orthopteran abundance

A total of 2,178 individuals were recorded across both transect survey periods. Most of the recorded individuals belonged to *P. parallelus* (54.6%), followed by *C. biguttulus* (21.5%), *C. brunneus* (12%), and *M. parapleurus* (5.5%). A minority of recorded individuals belonged to *R. roeselii* (4.8%), *T. viridissima* (0.4%), *R. nitidula* (0.3%), *C. fuscus* (0.2%), *C. dorsatus* (0.2%), and *C. albomarginatus* (0.1%). On average, 54 (± 36) Orthoptera individuals per 200 m² were recorded across all 20 sites within the UVS. The maximum number of individuals recorded at a single site was 134 per 200 m², while the minimum was 13 per 200 m².

Comparison of PAM and transect method

The number of orthopteran species detected by each method at the different sites is shown in Fig. 3a. The RMA slope was 0.74 (95% CI: 0.26–1.62), which includes 1 and therefore does not differ significantly from the 1:1 line at $\alpha=0.05$. The intercept was 0.53 (95% CI: -3.51–2.73), which includes 0 and likewise shows no significant deviation from the 1:1 line at $\alpha=0.05$. These results indicate that species richness estimates from the two methods were positively related along the 1:1 line (Fig. 3a). A Wilcoxon rank-sum test revealed a significant difference ($p=0.044$) in the number of detected species, with a higher mean number recorded by transects (mean=4.6) compared to daytime acoustic recordings (mean=4).

At the species level, the number of detections for each species and method across all 20 sites is shown in Fig. 3b. Both methods detected *P. parallelus*, *C. biguttulus*, *C. brunneus*, *R. roeselii*, *S. scalaris*, *C. albomarginatus*, and *C. dorsatus*, although some of these species were more frequently recorded by daytime PAM at sites where they were missed during transects. *O. viridulus*, *C. dispar*, *S. lineatus*, and *T. cantans* were detected only in daytime recordings and were missed during transects. In contrast, *M. parapleurus*,

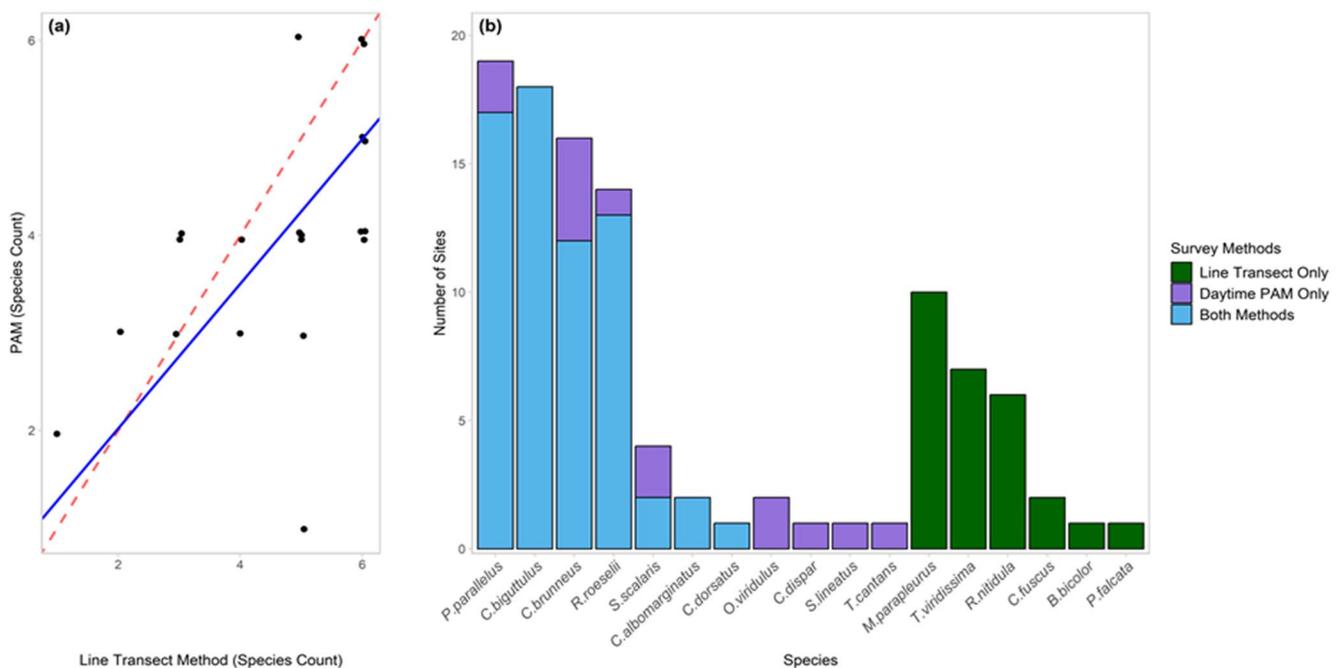


Fig. 3 Comparison of daytime PAM and the Line Transect Method. **a** Number of orthopteran species detected by the Line Transect Method and by the daytime Passive Acoustic Monitoring (PAM) method. The dashed red line indicates the 1:1 diagonal, and the solid blue line represents the Reduced Major Axis (RMA) regression. **b** Number of sites at which each orthopteran species was recorded using the Line Transect Method, daytime Passive Acoustic Monitoring (PAM), or both

T. viridissima, *R. nitidula*, *C. fuscus*, *B. bicolor*, and *P. falcata* were recorded exclusively during transects and not in the daytime acoustic recordings. Detailed species detection results for each site and method are presented in Table S2 and will be further discussed in the Discussion section.

Environmental factor analysis

Orthopteran species richness and abundance

For orthopteran species richness (OSR), the model with the lowest AICc score included plant species richness (PSR) as the explanatory variable. The model revealed a positive relationship between PSR and OSR, with the number of orthopteran species per site increasing as plant species diversity within the UVS increased, though this trend only approached statistical significance (Estimate=0.106, SE=0.052, $t(18)=2.06$, $p=0.055$; Fig. 4). The model explained 19% of the variation in OSR ($R^2 = 0.19$, adjusted $R^2 = 0.145$), with a residual standard error of 1.91 on 18 degrees of freedom ($F(1,18)=4.22$, $p=0.055$).

For orthopteran abundance (OA), the model with the lowest AICc score included management (M) and the number of understory vegetation strips (NOU) as explanatory variables, with the dependent variable log-transformed. The model showed that abundance was lower on conventionally

managed sites compared to organically managed ones (Estimate = -0.56 , SE=0.29, $t(17) = -1.95$, $p=0.069$), corresponding to an average reduction of about 56% (Fig. 4). The number of UVS also had a negative, but non-significant, effect on OA (Estimate = -0.068 , SE=0.052, $t(17) = -1.31$, $p=0.208$). Overall, the model explained 21% of the variation in OA ($R^2 = 0.21$, adjusted $R^2 = 0.12$), with a residual standard error of 0.61 on 17 degrees of freedom ($F(2,17)=2.27$, $p=0.134$).

managed sites compared to organically managed ones (Estimate = -0.56 , SE=0.29, $t(17) = -1.95$, $p=0.069$), corresponding to an average reduction of about 56% (Fig. 4). The number of UVS also had a negative, but non-significant, effect on OA (Estimate = -0.068 , SE=0.052, $t(17) = -1.31$, $p=0.208$). Overall, the model explained 21% of the variation in OA ($R^2 = 0.21$, adjusted $R^2 = 0.12$), with a residual standard error of 0.61 on 17 degrees of freedom ($F(2,17)=2.27$, $p=0.134$).

Discussion

The aim of this study was (i) to test passive acoustic monitoring (PAM) for assessing orthopteran richness and (ii) to identify factors influencing their richness and abundance on agroforestry fields. The results are discussed in the following sections, but it should first be noted that three orthopteran species (*B. bicolor*, *C. fuscus*, *P. falcata*) classified as vulnerable, and two species (*C. dispar*, *R. nitidula*) classified as potentially endangered (Monnerat et al. 2007) were recorded on silvoarable agroforestry sites. As the loss of habitat quantity and quality is assumed to be the primary cause of the decline in orthopteran species richness (Poniatowski et al. 2024), it can be assumed that silvoarable agroforestry sites may support vulnerable orthopteran species by

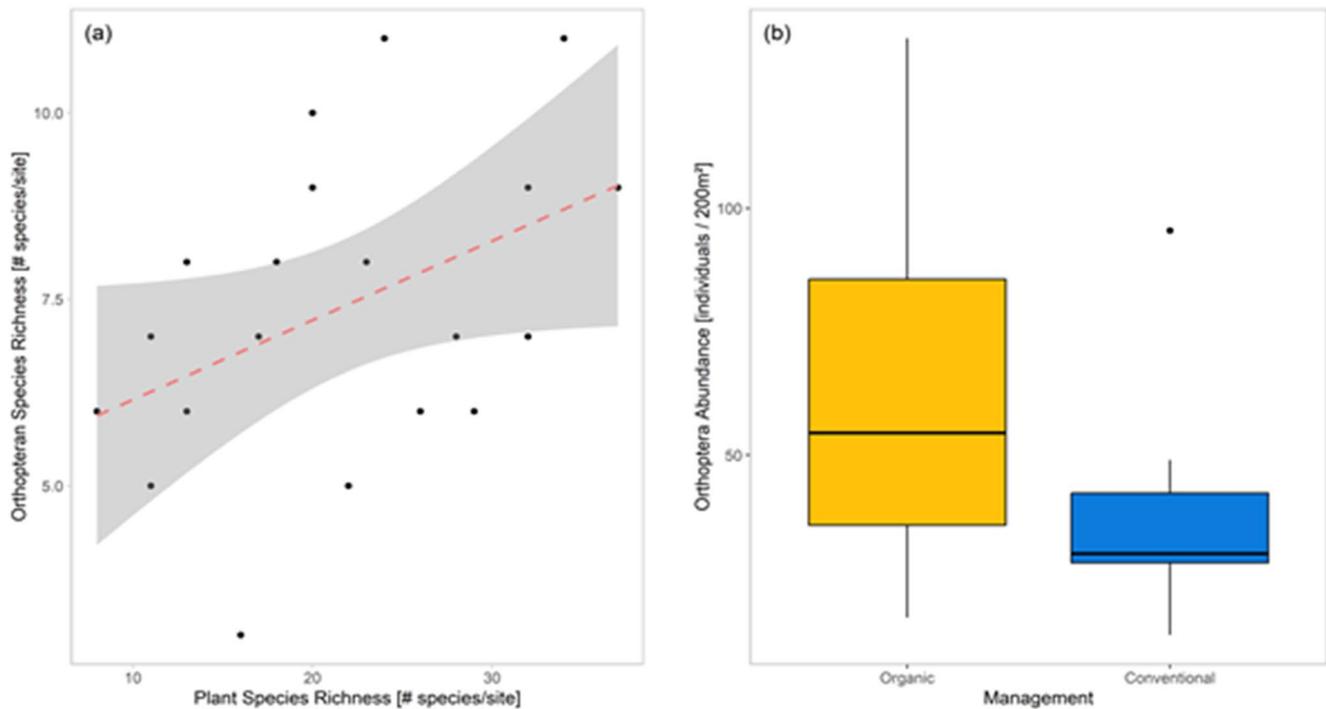


Fig. 4 Environmental factors for orthopteran species richness and abundance in agroforestry systems. **a** Orthopteran species richness plotted against plant species richness. The red dashed line shows the fitted linear regression, with the grey region indicating the 95% confidence interval; **(b)** Orthopteran abundance (individuals per 200 m²)

increasing the availability of potential habitats within the agricultural landscape.

Comparison of PAM and transect method

Across all study sites, the two methods did not yield the same number of orthopteran species, as revealed by a significant Wilcoxon rank-sum test. However, PAM detected a number of species comparable to the transect method. This is supported by the RMA regression, which showed no significant difference in either the slope or the intercept relative to the 1:1 line, indicating high overall agreement between the two methods. These results suggest that PAM captures similar trends in orthopteran biodiversity within agroforestry systems (Fig. 3a). These findings align with those of Bennett et al. (2025), who applied the same acoustic approach in non-agroforestry ecosystems using identical recording devices. The following sections discuss the identified strengths and weaknesses of PAM compared to the transect method, unexpected results, and its limitations.

A notable strength of daytime Passive Acoustic Monitoring (PAM) is its ability to detect orthopteran species that are easily overlooked during daytime transect surveys. In this study, PAM detected species such as *R. roeselii*, *S. lineatus*, and *C. dispar* at sites where they were not observed

in organically and conventionally managed agroforestry sites. Boxes represent the interquartile range (IQR), horizontal lines indicate medians, whiskers extend to $1.5 \times$ IQR, and points beyond whiskers are shown as outliers

during transect walks. Several of these species exhibit cryptic behavior (*R. roeselii*, *C. dispar*) or occur at low population densities (*S. lineatus*) (Baur et al. 2006), reducing their likelihood of detection during transect surveys. The non-invasive nature of PAM therefore offers a clear advantage in detecting such species. This finding is consistent with previous studies demonstrating the effectiveness of acoustic monitoring in identifying rare or elusive species (Riede 1998).

Despite its strengths, PAM showed weaknesses, as some species were not detected acoustically during daytime. For example, *T. viridissima*, *R. nitidula*, and *P. falcata* were recorded exclusively during daytime transect surveys but were absent from PAM daytime recordings (Fig. 3b). These species are classified as nocturnal and typically stridulate only at night (Roesti and Keist 2009). As this method comparison was based solely on daytime recordings, their absence from the acoustic dataset was expected. However, this limitation could be addressed by extending the recording protocol to include nocturnal sampling periods. Furthermore, daytime PAM missed species such as *C. albomarginatus*, *B. bicolor*, and *C. fuscus*. The calls of *C. albomarginatus* closely resemble those of *C. brunneus*, and those of *B. bicolor* resemble *R. roeselii* (Roesti and Keist 2009), increasing the risk of misidentification. As for *C.*

fuscus, this species appears usually in low abundance and stridulates quietly (Roesti and Keist 2009), making it likely that it could not be heard or did not appear clearly on the oscillogram due to background noise or other factors. When analysing audio recordings, noise is a major problem, but there are many reasons for this noise and thus very different methods of dealing with it. One reason could be attributed to louder and more abundant orthopteran species, such as *C. biguttulus*, *C. brunneus*, and *P. parallelus* (Roesti and Keist 2009). These species may drown out those species with lower abundance and quieter stridulation sounds. Additionally, the noise issue could be linked to the technical specifications of the AudioMoth device, particularly its microphone. According to the manufacturer, the device has a signal-to-noise ratio of 44.2 dB, meaning the microphone produces self-noise in the absence of ambient sounds (Darras et al. 2020). This rather high self-noise is a possible reason for the difficulty to detect quieter orthopteran species. According to Darras et al. (2020), the recording time can be increased to address this issue. This was also supported by the results of (Bennett et al. 2025), which showed that the total number of species detected at each site tended to increase with longer recording times. To address the increasing number of recordings, automated computer-aided identification software could offer a promising solution (Newson et al. 2017; Faiss & Stowell, 2023, Bennett et al. 2025).

Furthermore, some results are contradictory: only a few species were detected by both methods (Table S2). At site 5, PAM failed to detect most species, likely due to the mowing regime of the UVS. It can be assumed with high certainty that the UVS was mown at the beginning of the recording period, causing most orthopterans to either die or disperse. At sites 19 and 11, PAM failed to detect dominant species recorded during the transects, such as *C. biguttulus*, while it did detect species like *S. scalaris*, *T. cantans*, and *O. viridulus* (Fig. 5, Table S2), which are more typically found at higher altitudes (Baur et al. 2006).

However, PAM has also its limitations. Firstly, PAM is limited to detecting only stridulating orthopteran species. As a result, *M. parapleurus* was not detected by PAM at any of the sites (Fig. 3b), as this species does not stridulate (Roesti and Keist 2009). Secondly, PAM does not allow for the estimation of abundance. Thirdly, PAM provides limited information on the exact location of detected species. For quieter species, however, this limitation is less critical, as their presence near the recording site can be reasonably inferred if their calls are recorded. In case of louder species such as *T. viridissima*, whose stridulation can be heard from up to 200 m away (Fischer et al. 1997; Roesti and Keist 2009), it becomes difficult to determine whether they are present within the site or simply nearby. On the other hand, orthopterans are mobile organisms (Marini et al. 2012), and

it can be assumed that these species move through various habitats suggesting they could still be considered part of the studied ecosystem even if detected from a distance.

The results of this study are limited to the use of AudioMoth recorders with a recording protocol consisting of 10 days, with two hours of recording each day after midday. Within these limitations, the study demonstrated that PAM can reliably detect a similar number of orthopteran species, highlighting its potential as a comparable method to the line transect method for assessing orthopteran species richness in agroforestry systems. The PAM method demonstrates its strength in detecting cryptic or low-abundance species compared to daytime transects, making it a complementary method. However, PAM also revealed weaknesses, likely missing some species due to noise issues, not allowing for the estimation of abundance, and showing limitations in detecting non-stridulating orthopteran species.

Environmental factor analysis—orthopteran species richness

The study is limited to relatively young agroforestry sites. Taking these limitations into account, the results showed that, among all analysed variables, plant species richness within the agroforestry system is the most important factor in explaining orthopteran species richness.

The positive correlation between plant species richness in the UVS and orthopteran species richness aligns with similar patterns observed in grassland ecosystems (Ingrisch and Köhler 1998) and highlights the potential of enhancing plant diversity within UVS to support orthopteran species richness. However, a direct link to increased food availability cannot be established, as none of the orthopteran species detected in the UVS are strictly dependent on specific plants for their diet (Ingrisch and Köhler 1998). Additionally, certain species detected within the UVS, such as *C. dispar*, *P. falcata*, and *C. fuscus*, rely on specific plant species for oviposition and select habitats accordingly (Ingrisch and Köhler 1998). This may explain the observed increase in orthopteran species richness with higher plant species diversity.

Vegetation not only provides fodder and oviposition substrates but also constitutes a structural habitat. In particular, vegetation height and density are considered key habitat factors for orthopterans (Gardiner et al. 2002; Gardiner and Hassall 2009). Different orthopteran species are adapted to a range of vegetation structures: some prefer tall, others shorter vegetation; some live in dense vegetation, while others prefer minimal soil cover (Sanger 1977). Increased plant species richness within the UVS likely enhances also vegetation structural diversity, which may support a broader range of orthopteran species and could explain the observed

results. To gain a better understanding of the factor plant species diversity measurements of vegetation height could be included in future studies.

Environmental factor analysis—orthopteran abundance

The transect comparison of 20 relatively young agroforestry sites shows that management practices are the main factor influencing orthopteran abundance.

The results showed a non-significant trend toward decreased orthopteran abundance within UVS on conventionally managed agroforestry sites ($p=0.069$). In agroforestry systems, management practices primarily differ in plant protection and plant nutrition. However, it is likely that the pesticides or fertilizers were not applied solely to crop areas. As a result, UVS may have been exposed similarly to crop zones due to spray drift in liquid applications or mechanical limitations in fertilizer distribution.

In terms of plant protection, Bundschuh et al. (2012) demonstrated that orthopterans exhibit similar sensitivity to insecticides as standard test species used in arthropod risk assessments. Spray drift is a major source of pesticide exposure in off-crop habitats (Wang and Rautmann 2008). Therefore, it can be assumed that insecticides used in conventional farming may drift into UVS, exposing orthopterans through surface contact, ingestion, and contaminated egg-laying substrates (Ingrisch and Köhler 1998). This exposure may explain the lower orthopteran abundance observed within the UVS of conventionally managed agroforestry sites. Bundschuh et al. (2012) observed that orthopteran abundance comparable to grassland levels was only found in field margins wider than 9 m (Bundschuh et al. 2012). This may explain why the average UVS width of 2.7 (± 2.4) meters in our study showed no effect on orthopteran abundance.

Apart from plant protection, differences in fertilizer management may also explain our results. Mineral fertilizers, characterized by higher plant availability (Richner et al. 2017), promote early plant growth, which in turn delays the increase in soil temperature necessary for orthopteran egg hatching in the soil (van Wingerden et al. 1991). Furthermore, Schmidt (1986) observed reduced egg-laying in soils with higher mineral nitrogen content, as female orthopterans can detect soil nitrogen concentrations and tend to avoid such areas (Schmidt 1986; Ingrisch and Köhler 1998). Consequently, lower soil cover early in the season is expected to increase orthopteran abundance by raising soil temperatures. Analysing soil cover early in the season, along with soil nutrient content within the UVS, could provide further insights.

The model selection process identified the number of UVS per site as the second most influential factor affecting orthopteran abundance, although this effect was not statistically significant. This trend might be explained by the relative youth of the agroforestry sites, as orthopteran populations are likely not yet fully established.

Conclusion and outlook

This study demonstrates that Passive Acoustic Monitoring (PAM) using AudioMoth recorders can effectively identify most stridulating orthopteran species detected through line transects within agroforestry systems. These findings highlight the potential of PAM for future studies aimed at promoting orthopteran species across various ecosystems.

In addition, our results show that increasing plant species diversity within UVS can promote orthopteran species richness in agroforestry systems. Since vegetation structure is considered an important factor for the presence of orthopterans, future studies could account for vegetation height and cutting regimes within UVS. This could support the development of management guidelines for UVS. Additionally, the study identified the importance of organic management practices in increasing orthopteran abundance. Consequently, these findings suggest that organic management in agroforestry systems may play a key role in supporting biodiversity across multiple taxa, as orthopterans serve a vital function within the food web.

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Data availability The full dataset, including orthopteran species counts, abundance data, sound recordings, explanatory variables, and R code for analyses, is available upon request.

Declarations

Competing interests The authors declare no competing interests.

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